CAMBIUM AND VASCULAR DERIVATIVES OF GINKGO BILOBA

Lalit M. Srivastava [1]

NUMEROUS PAPERS AND MONOGRAPHS have been written about the habit, geographical and historical distribution, morphology and life history of *Ginkgo biloba* L. Most of this literature has been reviewed by Seward and Gowan (1900) and Sprecher (1907); and, in recent years, an extensive bibliography of papers published on different aspects of *Ginkgo* has been compiled by Franklin (1959). The structure of vascular tissues in the stems and roots of this plant has been described by several workers — in general, it resembles that of the conifers. However, there are some important differences, and certain anatomical details are not clear. The secondary xylem of *Ginkgo* is unique among gymnosperms in having parenchyma cells that accumulate druses of calcium oxalate, but whether these parenchyma cells occur in the axial tissue (Sprecher, 1907; Penhallow, 1907, p. 109–111) or also in the rays (Göppert, 1850, p. 266; Seward and Gowan, 1900) is not known. Tupper (1911) emphasized that the axial files of parenchyma cells containing druses were always in spatial contact with the rays. Penhallow (1907, p. 209) mentioned two types of tracheids in the xylem; but his observations were cursory and, to the best of my information, have not been reported in subsequent literature. Greguss (1955, p. 125) remarked on the irregular arrangement of tracheids in radial files of xylem, but he did not explain why it was so. The secondary phloem has been better described on the whole (Moeller, 1882; Strasburger, 1891; Sprecher, 1907), but the structure of fibers and the origin and distribution of albuminous cells are not clearly understood.

In order to understand thoroughly the structure of xylem and phloem and to determine the interrelationships of various cell types composing these tissues, detailed ontogenetic studies are essential. Since the xylem and phloem elements are derived from the cambium, a study of cambial phenomena is necessary also. The present investigation was undertaken, therefore, to study the developmental changes in the cambium and to relate these changes to the anatomical features of xylem and phloem. Relevant aspects of cambial activity are reviewed and described first; this is followed by the structure and ontogenetic relationships of the cell types in the vascular tissues.

MATERIAL AND METHODS

Material was collected from short shoots, young rapidly growing long shoots and the old trunk of a tree in Boston [2] in Dec., 1961, and from an old branch of a tree in Cambridge in April, 1962. An earlier collection made in Feb., 1958, included samples of long shoots from a young tree in the Botanical Gardens of the University of California at Berkeley.[3] Most of this material was killed and fixed in Craf III (Sass, 1951, p. 18), softened in equal parts of 95 per cent ethyl alcohol and hydrofluoric acid for 16–20 hours, embedded in celloidin, and sectioned on a sliding microtome. Serial cross, radial, and tangential sections were obtained. They were tied to slides with thread (see Cheadle and Esau, 1958), and stained with tannic acid-ferric chloride and lacmoid (see Cheadle, Gifford and Esau, 1953). The sections were mounted in Harleco resin. In addition, some material from Boston and Cambridge collections was sectioned fresh and some after being killed in Regaud's fluid (Davenport, 1960, p. 168). These sections were stained in different ways and served for checking some histological features. The slides of *Ginkgo* available in the wood collections of the Arnold Arboretum, Harvard University, were examined also. They served to confirm several details of xylem structure and as subjects for some photomicrographs of that tissue.

As is well known, the cambial initials produce xylem and phloem derivatives by periclinal divisions. The radial files of vascular elements derived by periclinal divisions in single cambial initials are termed tiers. Periodically, the cambial initials divide in an anticlinal plane to form two daughter initials, which in turn divide periclinally, and some cambial initials decline and are lost from the initial layer through maturation into a xylem or a phloem derivative. The radial extent of a tier comes to an end with an anticlinal division in, or with a decline and loss of, its cambial initial. A study of tiers, although laborious and time consuming, yields valuable data regarding the developmental changes in the cambium and the origin of vascular elements. For details of method, the reader is referred to Bannan (1950) and Srivastava (1962).

Tiers, particularly those formed by fusiform initials, were studied in the present work by the use of serial tangential and radial sections. They were studied in xylem as well as phloem. The xylem derivatives of fusiform initials showed some apical intrusive elongation during their differentiation (FIG. 3), but this elongation was not excessive and was sometimes absent. The study of tiers in phloem was rather difficult because the collapse and crushing of sieve elements and albuminous cells occurred close to the cambium and obscured the pattern of cell lineages. Consequently, the tiers were followed in phloem only as far as it was possible to do so with reasonable certainty.

The terms used in the present study have been defined earlier (see Cheadle and Esau, 1958; Srivastava, 1962). However, a few are defined again for clarity. The daughter initials, formed after an anticlinal division in a fusiform initial, grow intrusively at their tips until they attain the length common to the fusiform initials of that region; during this growth, they divide periclinally also. The initials that are growing are called *growing initials*; they become *regular initials* after they have stopped elongating. Their tiers are called *growing* and *regular tiers*, respectively. The fusiform initials that are lost from the cambial layer are called *declining initials* and their tiers *declining tiers*. The terms *phloic* and *xylary initial* are used to denote the daughter cells formed toward the phloem and xylem, respectively, after a periclinal division in the cambial initial. The phloic and xylary initials either directly, that is, without any further divisions, or after a few divisions, produce the various cell types in the vascular tissues.

OBSERVATIONS AND RESULTS

Cambium

In order to understand the activity of fusiform initials in the cambia of young and old stems, 50 tiers in each of the two kinds of stems were followed from the inner xylem to the cambium. A radial distance of ca. 0.8 mm. and almost two growth increments was involved in each case. The tiers were selected at random in the first section of the tangential series and I had no idea what would eventually happen to the fusiform initials of the tiers selected. The results of this study are shown in a diagrammatic manner in FIGURES 1 and 2. In these figures the horizontal lines represent tiers; a bifurcation means an anticlinal division in the fusiform initial and the end of its tier; a line that stops short of the cambial level means the end of the tier through the loss of the fusiform initial; and small oblique lines with numerals by their side represent the number of new ray initials added to the cambium. Vertical lines demarcate the growth increments.

A comparison of these two figures reveals that the number of anticlinal divisions per unit of xylem increment is higher in young than in old stems. In the young stem 19 initials divided anticlinally, and of the 38 daughter initials 4 divided again. In the old stem, in contrast, only 4 initials divided anticlinally. Taking all tiers that were followed, in the young stem there was a net increase of 5 initials, over the original 50, after 23 anticlinal divisions. In the old stem there was no increase in the number of fusiform initials because the number of new initials that was added by anticlinal divisions was balanced by the number of initials that was lost from the cambium. (These figures must not be interpreted to mean that in this sector of the old stem there was no increase in the number of fusiform and ray initials with increasing diameter of the wood cylinder. Probably there was such an increase, but it did not become apparent in the tiers that were followed through the short radial distance of xylem.)
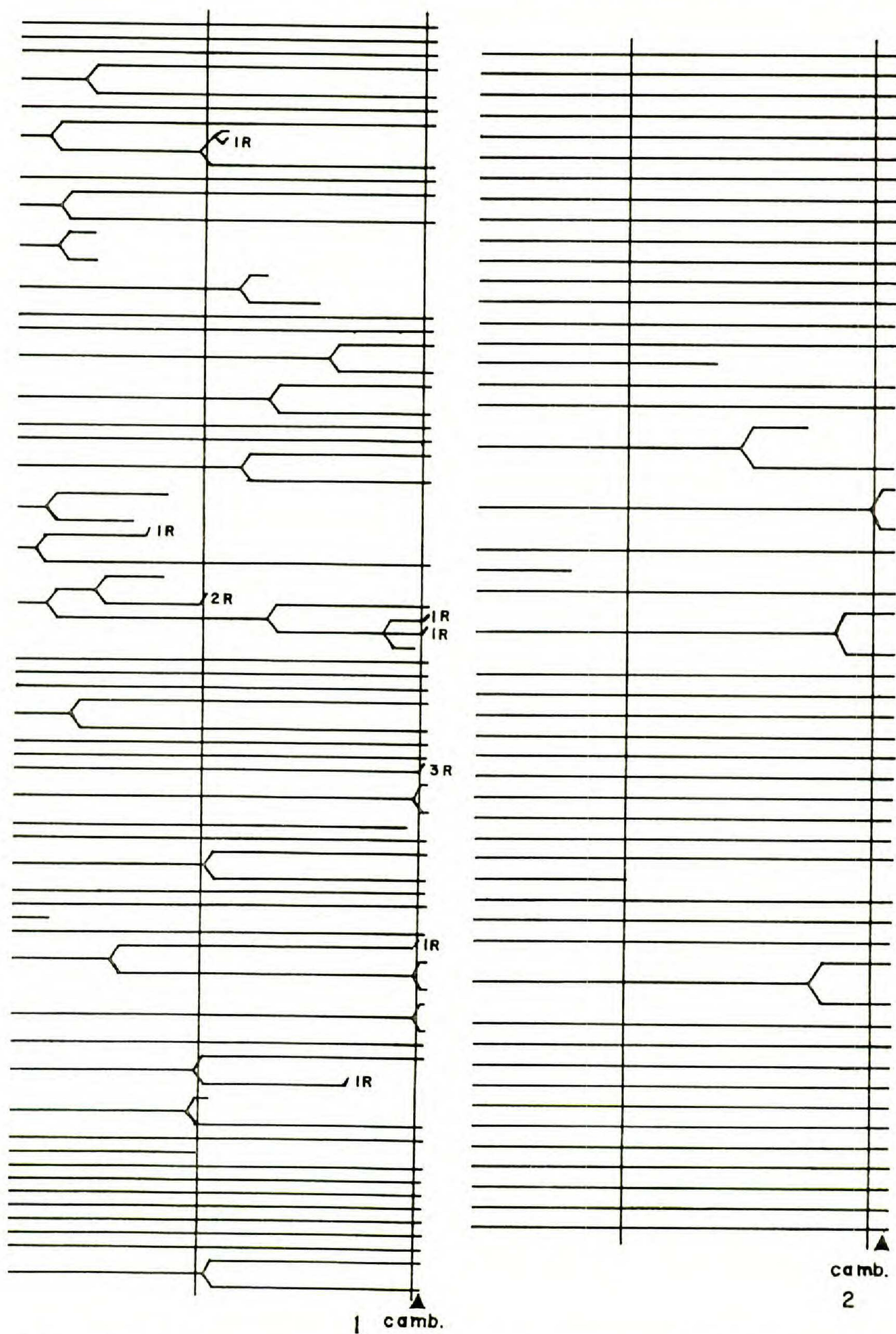
FIGS. 1, 2. Diagrammatic representation of the history of 50 fusiform initials and their daughter initials in a young (ca. 4 year old, FIG. 1) and an old (ca. 50 year old, FIG. 2) stem.

The results presented here are based on a very small sample and cannot be used statistically; however, they support the conclusion reached by Bannan (1960b) for conifer cambia that the frequency of anticlinal divisions and the survival of daughter initials are higher in young rapidly growing stems than in old stems.

It may appear from these figures that the relative frequency of anticlinal divisions in *Ginkgo* is less than in comparable material of conifer cambia (cf. Bannan, 1950, 1960a; Whalley, 1950; Srivastava, 1962). Among the 50 initials followed through almost two years growth, 27 initials in the young stem and 43 in the old stem divided only in the periclinal plane. (The initials that declined are omitted from this consideration.) It must be emphasized, however, that the results obtained in the present survey are based on a very small sample of the material of *Ginkgo* and the radial distances of xylem followed were not extensive. These results will have to be substantiated by a much wider sampling than was possible here before valid comparisons between the cambia of conifers and *Ginkgo* can be drawn.

The planes of anticlinal walls as seen in the cambium and as interpreted from the xylem derivatives show varying degrees of obliquity, but transverse or nearly transverse anticlinal walls seem to be rather rare. The oblique anticlinal walls may be very long, sometimes extending through one-fourth to one-third of the length of the original initial. The anticlinal divisions occur more or less near the middle of the dividing initial but in some cases, particularly in young stems, they are placed more toward one end and form daughter initials of unequal lengths.

During the elongation of daughter initials following an anticlinal division a curious phenomenon was noted. FIGURE 4 shows successive xylem derivatives of two fusiform initials. Only the tips of the derivatives are drawn and the derivatives of one initial are stippled. It will be noticed that the tips of the derivatives appear in different positions relative to one another at b and c. A simple explanation of this phenomenon would be that the xylem derivatives of the two fusiform initials elongated intrusively in different directions during their differentiation. If the intrusive elongation of differentiating tracheids is ignored, two other possibilities may account for the phenomenon. First, the fusiform initials of the two tiers underwent some shortening (see asymmetric periclinal divisions, below) after the periclinal divisions that produced the derivatives at b and elongated in different directions before they divided periclinally to produce the derivatives at c. Second, the tips of the two fusiform initials shifted their position relative to one another between the time they produced the derivatives at b and c. This explanation would involve actual "physical movement" of the tips of the two fusiform initials relative to one another. It was not possible to determine which of these explanations was true, but the phenomenon is indicative of the high degree of mutual adjustment among and between the fusiform and ray initials and their derivatives.

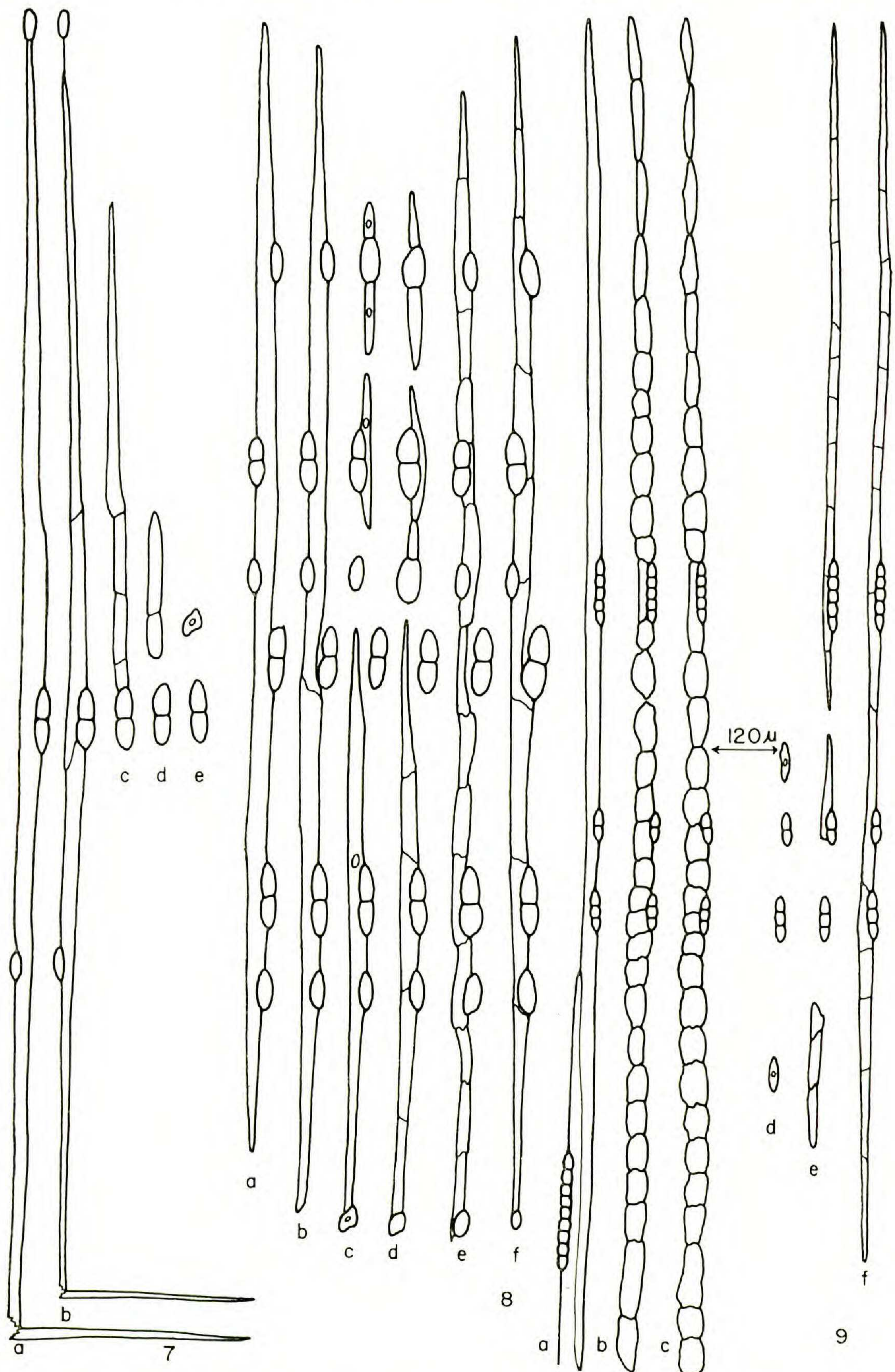The decline of fusiform initials in the cambium of *Ginkgo* occurs essen-
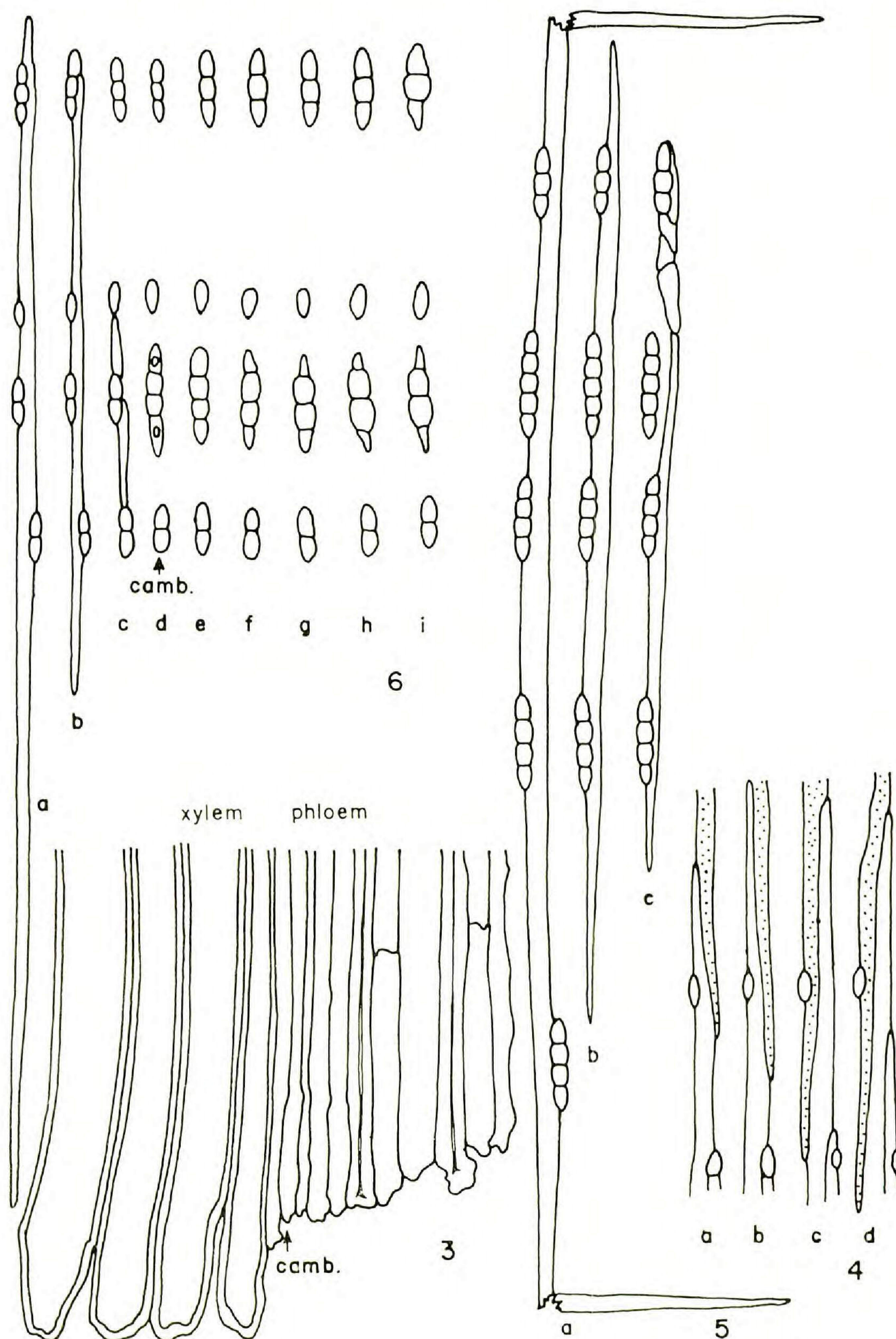
FIGS. 3–6. Selected tiers in radial and tangential view. 3, Old stem, radial view of a tier in xylem and phloem; only one end of the tier is drawn, × 195. 4, Young long shoot, tangential sections; successive tracheary derivatives of two fusiform initials, only the tips of the derivatives are drawn, × 95. 5, Old stem, tangential sections; successive xylem derivatives of a fusiform initial that declined without leaving any ray initials, × 95. 6, Young long shoot, tangential

tially in the same manner as described for conifers (see Bannan, 1953; Srivastava, 1962); and results either in a total loss of the initial from the cambial layer by maturation into a xylem or a phloem derivative, or in its conversion to one or more ray initials. The periclinal divisions in the declining initials are usually asymmetric and so oriented that the shorter cell is left in the cambial layer and acts as the initial for the next division. The results of these divisions are seen in the xylem and phloem and are marked by a progressive shortening of the succeeding derivatives in the declining tier. FIGURE 5 shows the last few xylem derivatives of a declining fusiform initial which was lost from the cambium without leaving any ray initial. FIGURE 6 shows a declining tier in xylem and the remnants of its initial in cambium, which appear as two new ray initials attached to the margins of a two-celled ray. The new ray initials yielded derivatives toward the phloem side only (FIG. 6, i–e).

In several instances, the declining fusiform initial divides transversely, or obliquely, one or more times and the individual segments are lost by maturation or undergo further shortening by asymmetric periclinal divisions. The individual segments may further divide transversely (transverse divisions of second order), the same process being repeated until nothing is left of the original initial, or parts of it remain in the cambial zone and become new ray initials. As a result of transverse segmentation of the fusiform initial and maturation of some segments and shortening of others, the declining tier breaks up into segments which may be discontinuous in the axial direction. The xylem derivatives shown in FIGURE 7 illustrate the segmentation of the declining initial, loss of the upper and lower segments, and the formation of a ray initial by the middle segment. As in FIGURE 6, the derivatives of this ray initial appeared only in the phloem (see one-celled ray at the bottom, FIG. 8, f–d). The decline of the tiers shown in FIGURES 6 and 7 could not be traced from the phloem side.

The decline of several tiers was followed from the phloem side and the relevant stages in xylem studied. The drawings in FIGURE 8, f–d, illustrate an anticlinal division in a fusiform initial followed by the decline of the upper daughter initial, which is present in the cambium (at c) as three axially discontinuous segments. The evidence for the anticlinal division is seen in the phloem and xylem derivatives at f and b, respectively. It will be noticed that the transverse segmentation and the breakup of the upper daughter initial into axially discontinuous portions is obvious in the phloem (e–d), but not in the xylem (b). The lower daughter initial was still present in the cambium; it is possible that it would have declined later. In FIGURES 9 and 14, likewise, the evidence for the breakup of the declining fusiform initial into axially discontinuous segments is seen in the phloem but not in the xylem. In FIGURE 9 two new ray initials are present in the cambium but, although the last axial derivative of the

sections; successive xylem derivatives (a–c) of a declining fusiform initial that left two new ray initials (shown with nuclei) in the cambium (d). The new ray initials produced derivatives only toward phloem (i–e), × 95.

FIGS. 7–9. Selected tiers drawn from tangential sections. 7, Young long shoot; successive xylem derivatives (a–d) of a declining fusiform initial which left one ray initial in the cambium (at e, cell with nucleus), × 120. 8, Young long shoot; successive xylem (a–b) and phloem (f–d) derivatives of a fusiform

declining fusiform initial occurred ca. 120 μ internal to the cambium, no derivatives of the new ray initials were encountered in the xylem.

From these examples and several others of tiers that were followed both in phloem and xylem, it seems that the transitional stages in the decline of fusiform initials are often more clearly seen in the phloem than in the xylem. But these stages occur in the xylem also (FIGS. 6, 7). It is possible, as Bannan (1953) has suggested, that the declining fusiform initials produce xylem and phloem derivatives in varying amounts — sometimes more phloem elements are produced, at other times more xylem elements.

During their decline, the fusiform initials and their segments may divide periclinally at irregular intervals with the result that their derivatives appear radially discontinuous. In the present study such radial discontinuities in declining tiers were recorded only in the xylem (FIG. 10). They were particularly evident between the last axial derivatives, and the first derivatives of the new ray initials (FIG. 11). Several such examples were recorded. That these new ray initials had been left in the cambium by the declining fusiform initial was supported by the study of other declining tiers both in the phloem and xylem (FIGS. 8, 9, 14) and by the presence of transitional stages in the xylem (FIGS. 6, 7, 10). The observation of declining fusiform initials in the cambium further supported this conclusion. Possibly, in these instances of radial discontinuity between the last axial and the first radial derivatives, the declining fusiform initials and their segments did not produce any xylem derivatives after their length had fallen below a certain value — they produced only phloem derivatives until they were converted to ray initials.

Sometimes the early derivatives of newly established ray initials are produced toward phloem only (FIGS. 6, 7 and 8). Whether these ray initials would have produced xylem derivatives at a later date could not be determined. It is, of course, possible that some ray initials produce derivatives toward phloem only and form what are known as phloem rays.

Reference has been made earlier to anticlinal divisions that set off daughter initials of unequal lengths. Such divisions were very common in the material of young stem. The shorter initials often declined and were converted to ray initials, or were lost by maturation into xylem or phloem elements.

The occurrence of radial divisions, in which the dividing wall twice intersects the same radial wall, near the middle of fusiform initials was recorded in the cambium and interpreted from a study of xylem and phloem

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initial which divided anticlinally. The upper daughter initial declined and was present in the cambium as three axially discontinuous segments (at c, cells with nuclei), $\times$ 120. 9, Old stem; successive xylem (a–c) and phloem (f–e) derivatives of a fusiform initial which declined and left two new ray initials in the cambium (at d, cells with nuclei). A radial distance of 120 μ intervened between the last xylem derivative (at c) and the cambium (at d); during this time neighboring fusiform and ray initials produced xylem derivatives. The anticlinal division represented in the xylem derivative at a was picked up in the phloem derivative that occurred ca. 80 μ external to the derivative at f, $\times$ 60.
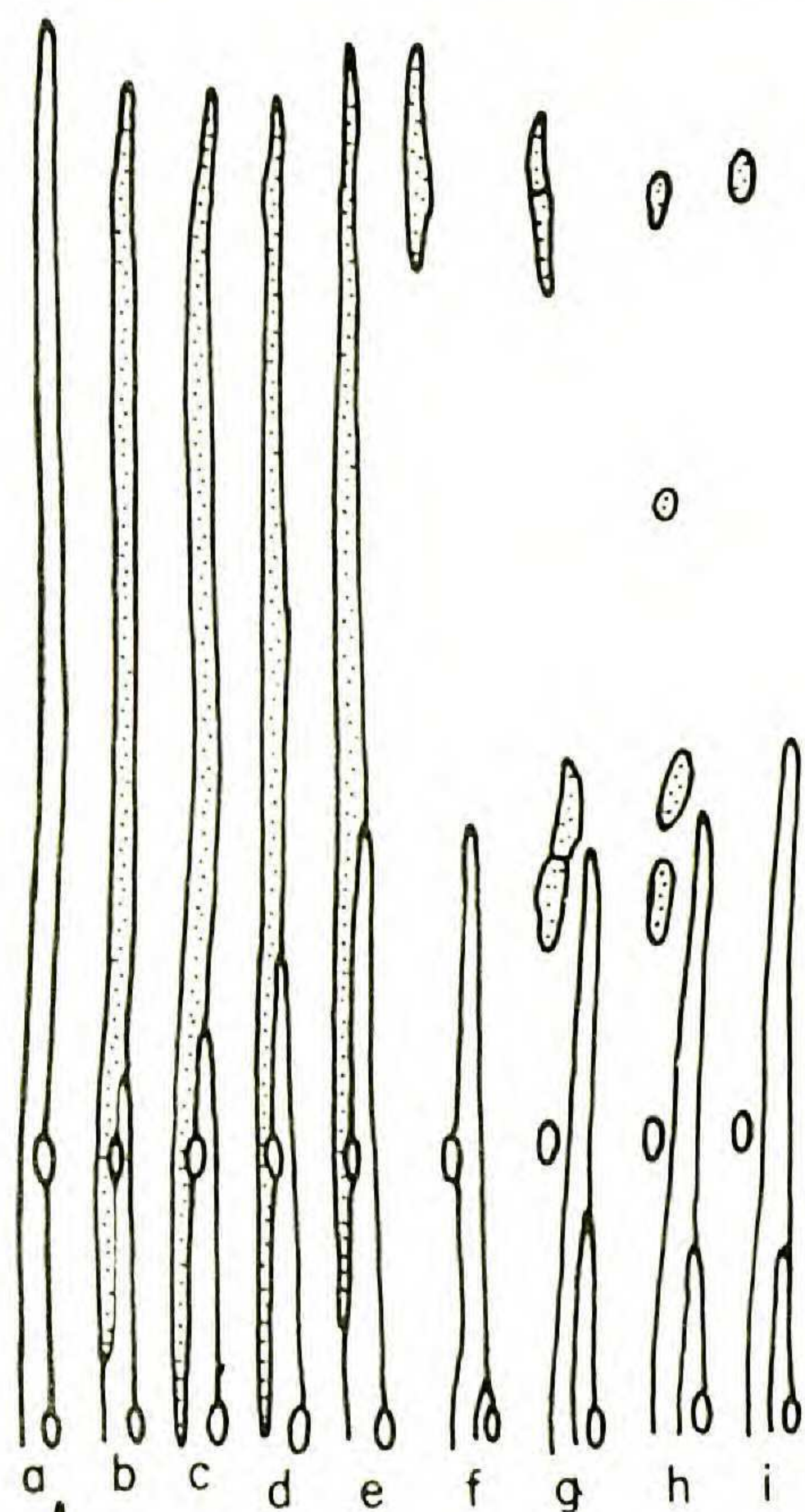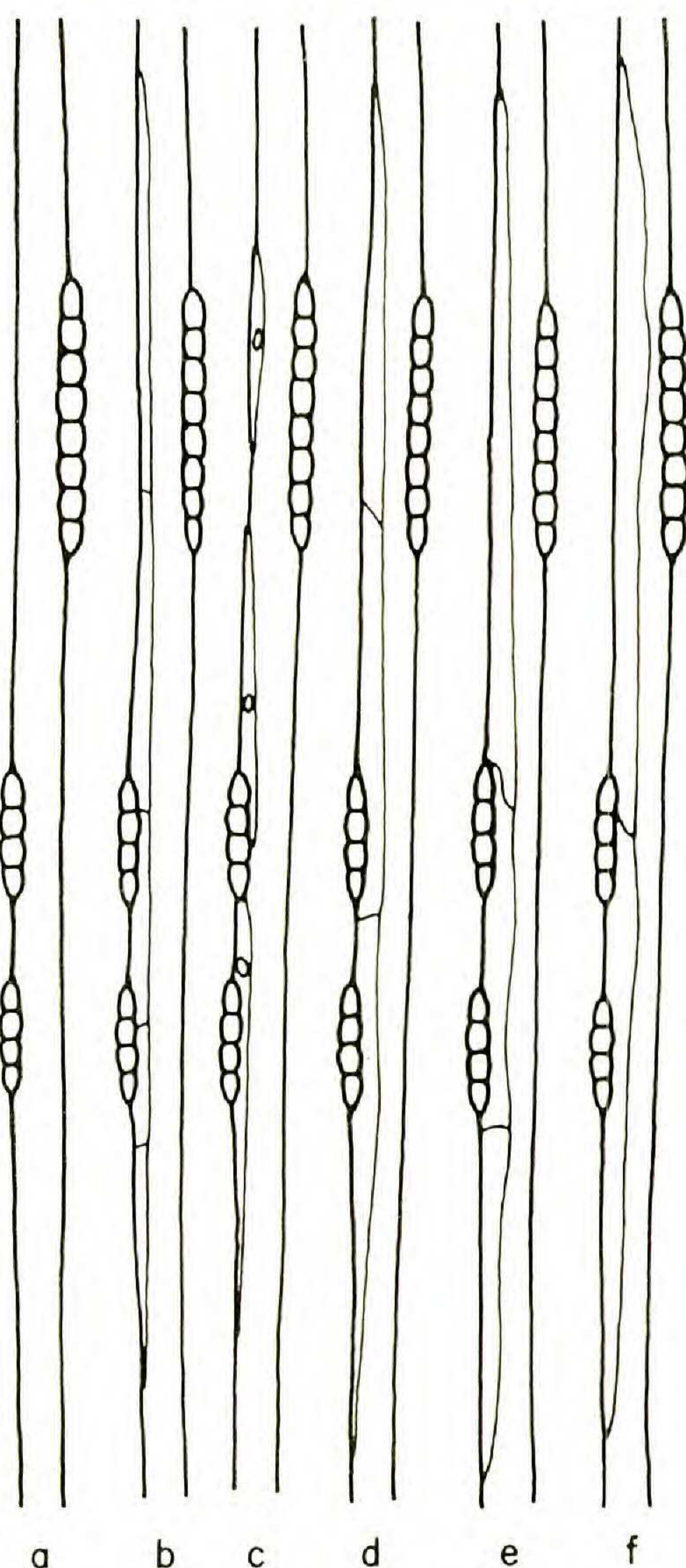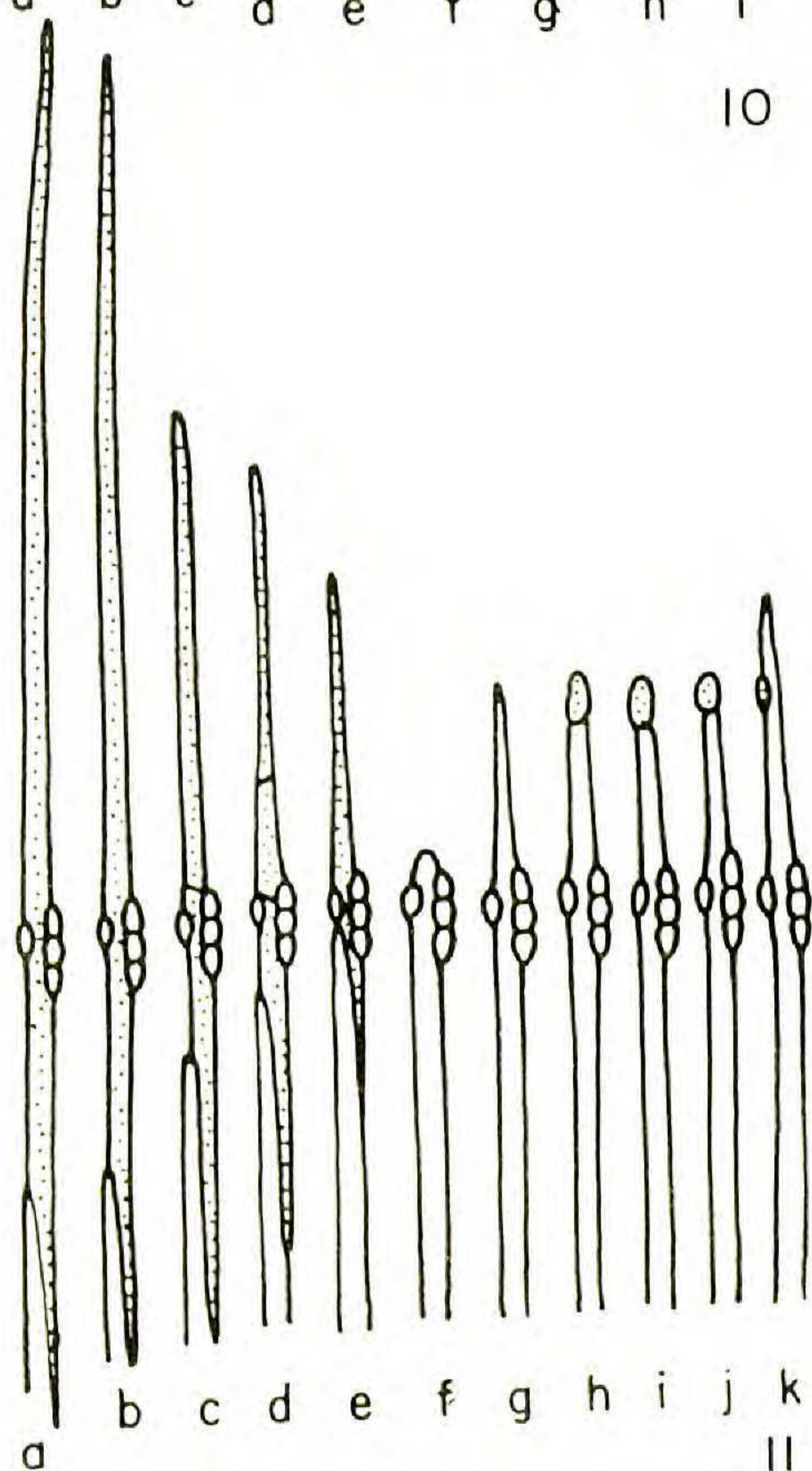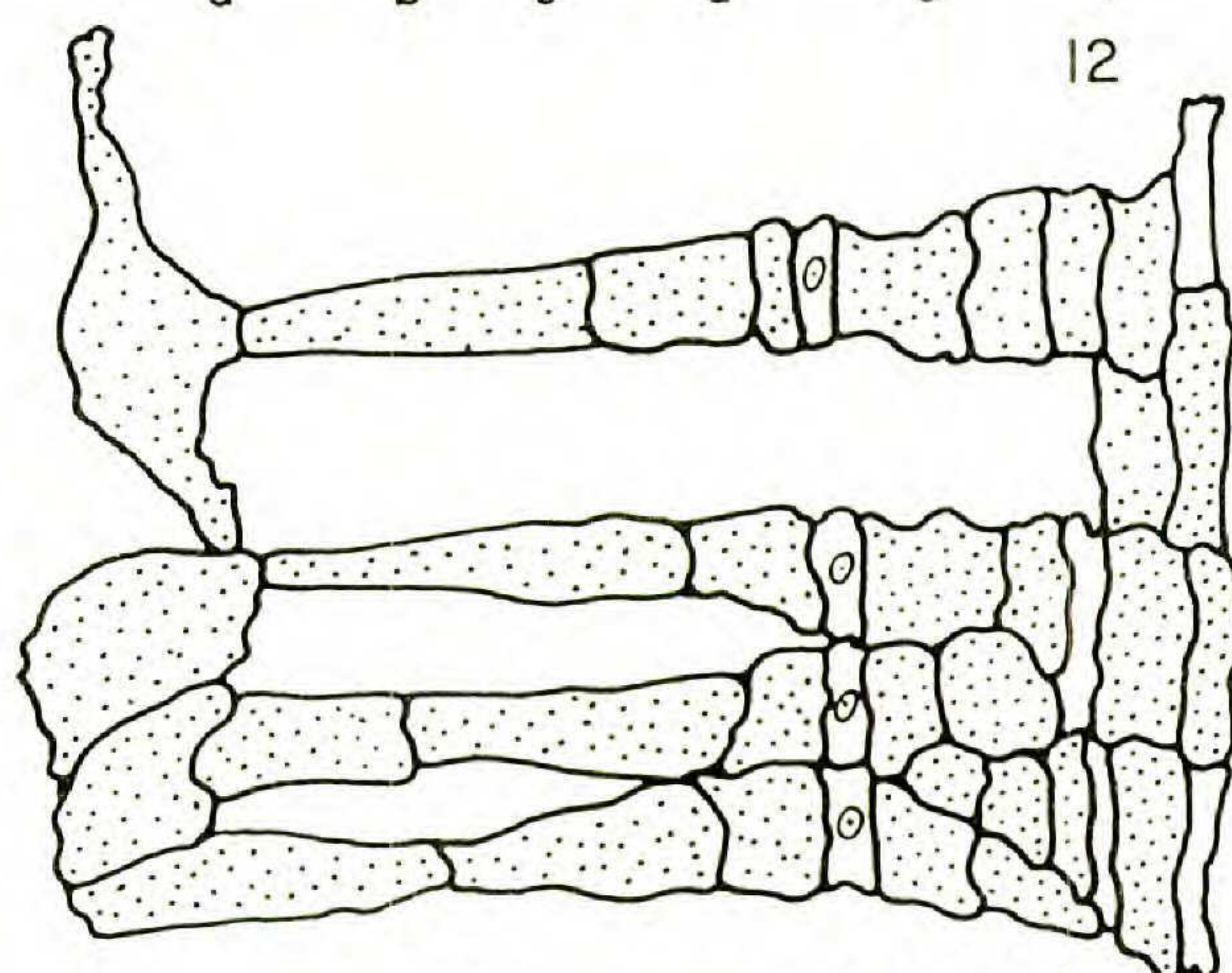
FIGS. 10–13. Selected tiers in tangential and radial view. 10, Young long shoot, tangential sections; successive xylem derivatives (stippled) of a declining tier and a ray. The figure also shows radial discontinuities between the derivatives of the declining tier. The derivatives of the subjacent tier are shown also,

(FIG. 12). Only a few radial divisions were seen, however, and it was not possible to determine whether they led to the formation of ray initials. In the literature on conifers, new ray initials are reported to be formed in this manner (Bailey, 1920a; Barghoorn, 1940; Bannan, 1957).

Addition of new ray initials at the margins of existing rays is a constant source of an increase in the height of rays (FIG. 6). Parts of declining initials often occur near the middle positions of the rays, but these parts usually do not become established in the cambium as new ray initials. This phenomenon is responsible, in part at least, for the generally uniseriate arrangement of rays in *Ginkgo*. Similar observations were made earlier in the Pinaceae (Srivastava, 1962).

Xylem

The secondary xylem of *Ginkgo* shows discernible growth increments. But in some specimens the amount of late wood formed in a year may be small — limited to one or two tangential layers of cells — and the boundaries between successive growth increments not very obvious (FIG. 16). In these specimens the progressive decrease in the radial diameter of tracheids during the transition from spring to summer wood seems to be absent also. Apparently, these phenomena, like the ring width, vary with the growth conditions and the age of a plant. (For seemingly conflicting reports in the literature about the discernibility of boundaries between growth increments and the amount of summer wood formed in a year in *Ginkgo*, cf. Göppert, 1850, p. 54; Nakamura, 1882; Strasburger, 1891, p. 10; Sprecher, 1907; Penhallow, 1907, p. 209; Greguss, 1955, p. 125; Cheng, 1958.)

The tracheids, as is usual in gymnosperms, are long prismatic cells. Bailey and Tupper (1918) found that the average length of tracheids in *Ginkgo* increased from 0.9 mm. in the first annual ring to 3.5 mm. in increments more than 60 growth rings away from the pith. Some measurements of the length of tracheids in young long shoots and old stems in the present work yielded similar results. In a fossil specimen of *Ginkgo* wood (courtesy of Prof. E. S. Barghoorn, Jr.) the tracheids were as much as 8–9 mm. long. The age of the tree from which this sample came was, of course, unknown.

The tracheids have circular bordered pits in one or more rows on their radial walls. The tracheids of spring wood have only occasional pits on their tangential walls, whereas those of summer wood have them commonly. Some summer wood tracheids, particularly in the young stems,

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× 70. 11, Young long shoot, tangential sections; successive xylem derivatives (stippled) of a declining fusiform initial and the ray initial that it formed. The derivatives of the subjacent tier are drawn also, × 70. 12, Old stem, tangential sections; successive xylem (a–b) and phloem (f–d) derivatives illustrating a radial division in the fusiform initial. The shorter cell formed after the radial division declined and was present in the cambium (at c) as three axially discontinuous segments (shown with nuclei), × 80. 13, Old stem, radial view of part of a declining tier and ray in xylem and phloem. Starch-containing cells are stippled, albuminous cells in outline, cells in cambial zone with nuclei, × 150.

had one or more transverse walls which were distinctly pitted (FIG. 18).
The bordered pits in *Ginkgo* generally appear to have no torus on their
membranes. However, a small torus is discernible at high magnifications
in the membranes of unaspirated pit pairs (see also Wright, 1928). The
diameter of the torus is usually smaller than that of the pit pores. (For
details of pitting between tracheids and tracheids and rays, crassulae or
bars of Sanio, and trabeculae, see Kleeberg, 1885; Müller, 1890; Seward
and Gowan, 1900; Sprecher, 1907; Bailey, 1919, 1925; Kanehira, 1926;
Greguss, 1955, p. 126; Cheng, 1958.)

A peculiar phenomenon noted in the xylem of *Ginkgo* is the presence of
two more or less distinct types of tracheids in the spring wood. The two
types of tracheids differ in their cross sectional diameters, thickness of
their secondary walls, and the manner of pitting on their walls. For con-
venience, they are referred to as wide and narrow tracheids (FIGS. 17, 19).

The chief difference in the cross sectional diameters of these two tra-
cheids is in their radial dimensions. Occasionally, the narrow tracheids
have smaller tangential dimensions also. These overall size differences
in cross sections are accentuated because the narrow tracheids as a rule
have thicker secondary walls than the wide tracheids. With phloro-
glucin-HCl, however, the walls of these tracheids stain with equal in-
tensity (FIG. 17). The wide tracheids have circular bordered pits in one
or more rows along their radial walls, and well developed crassulae fre-
quently separate individual or groups of pits. These tracheids are con-
nected with the cells of the xylem rays by a combination of bordered pits
and primary pit fields. In contrast to the wide tracheids, the narrow
tracheids have very few pits on their radial walls, and these pits are gen-
erally confined to those areas of the wall that are in contact with the cells
of the xylem rays (FIGS. 19, 20).

The samples examined in the present study came from different trees
and were of different ages. Among these samples there was considerable
diversity with regard to the occurrence of narrow tracheids. They were
particularly common in old specimens with wide growth increments, and
rather poorly represented in young specimens (cf. FIGS. 21–23). They are
present in young specimens, however, and may be seen even in the first
one or two years of xylem growth. Within a growth increment, the nar-
row tracheids appear to be relatively more abundant in the wood formed
later in the spring.

The wide and narrow tracheids occur interspersed in the same radial
file — a variable number of wide tracheids alternating with an equally
variable number of narrow tracheids (FIGS. 17, 20, 21). These tracheids
are the usual xylem derivatives of growing and regular fusiform initials;
their lengths within a tier correspond to the length of the fusiform initial
responsible for that tier. Small differences in the length of tracheids within
a tier are common; these differences are probably related to the varying
degrees of intrusive apical elongation of the differentiating xylem tracheids.
No direct relationship is evident, however, between the extent of apical
elongation and the differentiation of narrow or wide tracheids. Within a

tier some narrow tracheids may be longer, others shorter, than the wide tracheids (FIG. 20).

The presence of wide and narrow tracheids within the same tier indicates that the differences between these tracheids are brought about during their differentiation. The difference in radial diameter of these tracheids is probably the result of differential expansion — the wide tracheids expanding more than the narrow tracheids. The difference in tangential diameter, when present, is more difficult to explain. Lateral compression, due to expansion of derivatives in adjacent tiers, seems to be most likely. Some tangential shrinkage is also possible. In some instances, a radial division in the xylary initial may also occur.

Several workers have recorded the presence of axial parenchyma cells in the secondary xylem of *Ginkgo*. Some of these cells accumulate druses of calcium oxalate. Among the samples that I examined, the occurrence of parenchyma cells was rather variable and seemed to be related to the age of the sample. In young twigs parenchyma cells may not be formed for the first 3–4 years of xylem increment. Later they are formed and store starch. Parenchyma cells with druses of calcium oxalate generally do not appear until the 7th or 8th year of xylem growth.

The analysis of tiers revealed that the differentiation of parenchyma cells in the axial system is related primarily to the decline of fusiform initials. It is, of course, possible that some derivatives of growing and regular initials differentiate as parenchyma strands, but such an occurrence seems to be rare. The xylem derivatives of declining fusiform initials often become transversely divided and form strands of cells. These transverse or oblique divisions apparently occur in the xylary initials. They are more common in the declining tiers of old stems than of young, possibly because the fusiform initials, and hence the xylary initials, are much longer in the older material. Some of these cells in the declining tiers acquire pitted secondary walls like ordinary tracheary elements. Other cells remain parenchymatous.

In young twigs the xylem derivatives of declining tiers differentiate predominantly as tracheary elements, although some parenchyma cells storing starch may be formed also. In older material, some cells of declining tiers differentiate as tracheary elements, others as parenchyma cells storing starch, and still others accumulate druses of calcium oxalate (FIGS. 15, 21, 25, and 26). The cells that accumulate druses expand and become almost globular, and their differentiation is completed very close to the cambial zone (FIG. 27). The axial and the ray derivatives that are tangentially and radially adjacent to the expanding parenchyma cells become laterally displaced. Several declining tiers occur in the neighborhood of xylem rays — some segments of declining tiers may indeed be present between two axially adjacent rays (FIG. 15). In such instances it is difficult to distinguish between the ray cells and the derivatives of the declining fusiform initial and its segments in isolated tangential and radial sections; therefore it is possible to conclude that some ray cells accumulate druses. An examination of serial sections is necessary in these
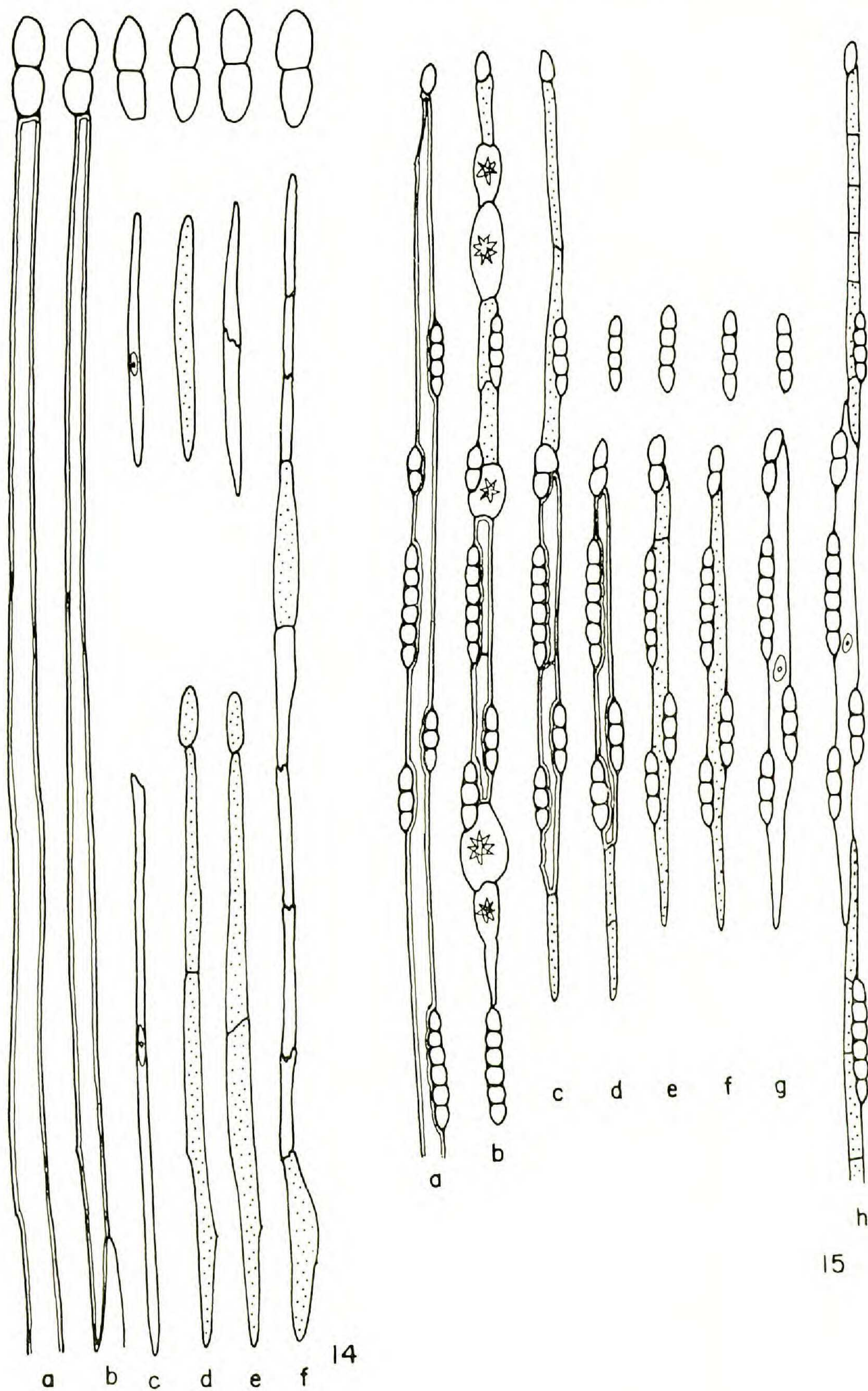
FIGS. 14, 15. Tangential sections showing derivatives in declining tiers. 14, Young long shoot; successive xylem (a–b) and phloem (f–d) derivatives, cambium at c, × 195. 15, Old stem; successive xylem (a–f) and phloem (h) deriva-

cases to determine the correct relationship between the axial and the ray elements.

The conversion of declining fusiform initials to ray initials is often accompanied by intermittent periclinal divisions toward xylem. Radial discontinuities frequently occur between the last axial and the first ray derivatives and, as a consequence, the xylem derivatives usually show a sharp and somewhat abrupt transition from an axial to a radial structure (Figs. 10, 11). This transition is reflected in the nature of the xylem derivatives also. The last axial derivatives store starch or druses of calcium oxalate, or may even be tracheary; however, the ray derivatives seem to store starch only (Fig. 13). In some instances of extended decline of fusiform initial represented in the xylem, it is possible that some early derivatives of ray initials accumulate druses. I have not recorded this phenomenon, however.

Phloem

The secondary phloem of *Ginkgo* consists of sieve elements, parenchyma strands and fibers in the axial system and the rays (Fig. 16). Fibers were absent in the secondary phloem of short shoots examined by me (Fig. 24), but it appears from the literature that this may not be generally true (cf. Seward and Gowan, 1900; Sprecher, 1907; Gunckel and Wetmore, 1946). As noted in the literature, however, druses were abundant in the phloem-parenchyma cells of the short shoots.

The sieve elements, as in gymnosperms, are elongated prismatic cells with sieve areas confined mostly to radial walls. The sieve areas in *Ginkgo* may be elliptical, oval, or round; but they are usually broken up into numerous small pore groups (Figs. 27, 28). Typical sieve plates are lacking and, in conformity with the accepted terminology (see Esau, 1950), the sieve elements in *Ginkgo* can only be considered as sieve cells. The sieve elements have thin walls; they lack the secondary, or nacré, wall typical of the sieve elements of Pinaceae (cf. Abbe and Crafts, 1939; Srivastava, 1962). The walls are weakly birefringent under polarized light.

As is typical for this type of cell, the mature sieve elements are enucleate. They have a thin layer of parietal cytoplasm and plastids. "Sieve element starch" that stains red with IKI is present.

The sieve elements are generally characterized by the presence of callose cylinders around the connecting strands in the sieve areas (see Esau, 1939, 1950). The material of *Ginkgo* examined by me was specially stained to detect the presence of callose. Only very small traces of callose were seen, however, even in the sieve elements close to the cambium. Most of the material was collected during periods of dormancy; the material from Cambridge was collected at a time when new leaves were just coming

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tives, cambium at g, × 95. Tracheary cells with double line, crystal cells with druses, starch-containing cells stippled, albuminous cells without nuclei, cells in cambial zone and undifferentiated cells with nuclei, ray cells in outline.

out. It is possible to assume, therefore, that in *Ginkgo* callose is present in the sieve elements only during periods of active growth, and that it disappears with the onset of dormancy. Detailed seasonal studies must be made, however, before the presence of callose can be related to the period of active growth.

Individual cells in phloem-parenchyma strands are distinguished on the basis of their contents, some contain starch, some accumulate druses of calcium oxalate, and some are specialized as albuminous cells (FIGS. 29–31). (For albuminous cells, see Strasburger, 1891, p. 55–62; Srivastava, 1962.) Some cells that store starch also accumulate tannins. These different cell types occur interspersed singly or in small chains in the same parenchyma strand. Occasional parenchyma strands may be composed of one type of cell only.

The cells that accumulate druses expand considerably. Strasburger (1891, p. 79–80) and Sprecher (1907) recorded the presence of crystal druses in some parenchyma cells of the youngest phloem, next to the cambium. I have not seen such an early deposition of druses in the phloem; although in xylem, as mentioned above, they are deposited in the youngest tissue. In the phloem of old stems that I examined the druses became evident ca. 8–10 layers of cells away from the cambium and it appeared that some starch-containing cells became modified as crystal-bearing cells.

The albuminous cells were distinguished in the present study by the lack of starch (FIG. 29) and by their collapse and crushing in the old phloem (FIGS. 27, 30). The albuminous cells, like the companion cells in angiosperms, are connected with the sieve elements by one-sided sieve areas (see Strasburger, 1891, p. 61, 65; Esau, 1939). However, as mentioned earlier, callose was not present in detectable quantity in the material of *Ginkgo* examined by me and, consequently, the sieve-area connections between the sieve elements and the albuminous cells were not very clear. The albuminous cells, like the sieve elements, have plastids and do not store starch that stains blue with IKI.

The fibers are elongated tapering elements that are flattened tangentially (FIGS. 16, 31). They usually have a very small lumen. Their thick secondary walls are distinctly lamellated and appear to be composed principally of cellulose. With phloroglucin-HCl they do not give a positive reaction for lignin (see also, Tobler, 1938). They are strongly birefringent under polarized light. Seward and Gowan (1900) mentioned that the fibers in *Ginkgo* are septate. I have not seen any evidence of transverse walls in these fibers. In tangential sections, because of their narrow radial diameter, the transverse walls of the radially adjacent parenchyma strands often appear to belong to the fibers. Also, the "slip lines" (Robinson, 1920; Frey-Wyssling, 1953), produced during sectioning, may be mistaken for transverse or oblique walls, or pore canals. A correct idea about the structure of fibers is obtained in macerations. In these preparations, cross walls are not observed; also, the pits seem to be very infrequent.

The sieve elements, parenchyma strands, and fibers are the usual deriva-

tives of growing and regular fusiform initials. Within a tier and among neighboring tiers, the production of sieve elements, parenchyma strands and fibers is somewhat irregular; and any resemblance to the four-cyclic alternation of the tangential bands of sieve cells, parenchyma strands, sieve cells, and fibers, typical of several species of Cupressaceae and Taxaceae, is rather vague (see also, Moeller, 1882, p. 33; Strasburger, 1891, p. 77–78; Seward and Gowan, 1900).

With the decline of fusiform initials, particularly in later stages of decline, the phloem derivatives are usually strands of parenchyma cells, some of which store starch while others differentiate as albuminous cells (Figs. 13, 14). Accumulation of druses in the derivatives of declining tiers was not observed, but it is possible. With the transition of declining fusiform initials and their segments to ray initials, the derivatives no longer differentiate as albuminous cells and only starch-containing cells are produced. But since the decline of fusiform initials and their conversion to ray initials is a continuous process, albuminous cells often appear among the earliest derivatives of ray initials; and in isolated tangential sections these albuminous cells may be interpreted as parts of rays.

DISCUSSION

The results obtained in the present survey indicate that the cambial phenomena in *Ginkgo*, that is, the planes of anticlinal divisions in fusiform initials, the growth and decline of fusiform initials, and the formation of new ray initials, are similar to those recorded in conifers (see Bailey, 1923; Bannan, 1953, 1957; Srivastava, 1962). Minor differences of a quantitative nature may perhaps be present. Thus, it is possible that the relative frequency of anticlinal divisions in a lineal series per unit of xylem (or phloem) increment is more in conifers than in *Ginkgo*. It is important here to discuss the role of anticlinal divisions in an increase in the girth of cambium.

As Bailey (1923) has mentioned, the multiplicative anticlinal divisions in fusiform initials are only one, among several, means by which the cambium is accommodated to the increasing girth of wood cylinder. Other means include an increase in length and tangential diameter of the fusiform initials and an increase in the number and tangential diameter of the ray initials. From the data presented by Bailey (1917, 1920b, 1923), Bannan (1960b), and in this paper, it seems reasonable to infer that in young stems of conifers and *Ginkgo* all the above-mentioned factors are operative in effecting an increase in the girth of the cambium. In old stems, however, the increase in length and tangential diameter of the fusiform initials and increase in the tangential diameter of the ray initials play only an insignificant role; the increase in the girth of cambium is effected primarily by an increase in the number of fusiform and ray initials. To achieve this increase in the number of fusiform and ray initials, anticlinal divisions are necessary.

The work of Bannan (1950) and Whalley (1950) on conifer cambia has shown that the number of anticlinal divisions in fusiform initials far exceeds the number actually required to accommodate the cambium to increasing diameter of the wood cylinder, and is accompanied by the loss of a large number of new initials. Thus, it is only a very small percentage of anticlinal divisions that is directly involved in increasing the girth of the cambial cylinder. It is of interest in this connection to recall that Priestley (1930) calculated from the data given by Bailey (1920b) that individual fusiform initials needed to divide anticlinally only once every fifteen years to accommodate the cambium to the increasing diameter of wood cylinder. These calculations have only a theoretical significance. However, they do emphasize that a high frequency of anticlinal divisions, as is seen in the conifer cambia, is not really essential for adjusting the cambium to the increasing circumference of wood cylinder. It is conceivable, therefore, that quantitative differences in the frequency of anticlinal divisions in fusiform initials may exist between the cambia of different plants. But large quantities of comparable material must be examined before such differences, if they are present, would be revealed.

Since the anticlinal divisions in fusiform initials of conifer cambia occur at a frequency far greater than is actually required, one wonders at the possible significance they might have, besides the fact that they result in an increase in the number of cambial initials. Bannan (1960a, b) has discounted the possibility that the frequency of anticlinal divisions may be directly related to the growth rate of the stem or to the length of the fusiform initials. He has concluded that the frequency of anticlinal divisions in fusiform initials apparently is geared neither to the circumferential expansion nor to the number of periclinal divisions in the cambium, but rather seems to be related to linear radial increment as determined by periclinal divisions both in cambial and xylary initials. It is possible to consider in this connection a role of anticlinal divisions that has not been mentioned so far. The anticlinal divisions confer upon the cambium a greater degree of plasticity than is possible with periclinal divisions (symmetric and asymmetric) and intrusive apical elongation only. Frequent anticlinal divisions and the loss of large portions of the new initials are phenomena of great significance in the mutual adjustments of the cambial initials and their derivatives. They are also of significance in adjusting the cambium to changes in the growth conditions of a plant. This increased degree of plasticity attained as a result of anticlinal divisions in the fusiform initials may have had a survival value in the course of evolution.

In the literature on the cambia of gymnosperms, new ray initials are reported to be formed by cutting off of large or small segments from the fusiform initials [4] (Velten, 1875; Schmidt, 1889; Klinken, 1914; Bailey, 1920a; Barghoorn, 1940; Braun, 1955). The divisions that separate these new ray initials may be radial, transverse, or of various degrees of

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[4] New ray initials are also formed by transverse, or anticlinal, divisions in existing ray initials.

obliquity and may occur near the middle or near one end of the fusiform initial. The ontogenetic work of Bannan and his associates (Bannan, 1950, 1953; Bannan and Bayly, 1956) and myself (Srivastava, 1962) has clarified the details of this process. As has been mentioned earlier, several fusiform initials are lost entirely, or in part, from the cambial zone. This loss, or decline, of fusiform initials is frequently brought about by a combination of asymmetric periclinal divisions and transverse segmentation. As a result, small segments of the original fusiform initial are left in the cambial zone and act as new ray initials. Ray initials are also formed by radial divisions in the fusiform initials — the shorter cells frequently persisting in the cambium as new ray initials.

These observations on the conifer cambia have been further substantiated in the present study. A few points may be emphasized briefly, however. In several instances of decline, the stages in the conversion of fusiform initials and their segments to ray initials are better represented in the phloem than in the xylem (FIGS. 8, 9, and 14). Also, occasionally, the first derivatives of new ray initials are produced only toward phloem (FIGS. 6, 7, and 8). Comparable literature, relating the extent of declining tiers in the xylem with that in the phloem, is lacking. But from the data presented here and my limited observations in the Pinaceae (Srivastava, 1962), it appears that during the transition of several fusiform initials and their segments to ray initials, periclinal divisions occur predominantly toward phloem and intermittently toward xylem. As a result, radial discontinuities appear in the xylem not only among the derivatives in the declining tier (FIG. 10) but also between the last axial derivatives of the declining fusiform initials and the first radial derivatives of the new ray initials (FIG. 11). These phenomena would explain the somewhat abrupt beginning of rays described by Bannan (1934) in the secondary xylem of *Ginkgo*.

The general resemblance of the secondary xylem and phloem in the long shoots of *Ginkgo* to those of conifers is obvious. There are some striking differences, however. These differences include the presence of narrow tracheids and crystal-bearing parenchyma cells in the xylem and cellulose fibers and crystal druses in the phloem. It must be pointed out in this connection that the presence of crystal druses in phloem and the manoxylic structure of the short shoots of *Ginkgo* are features shared by the cycads (see Mettenius, 1861; Strasburger, 1891, p. 154; Seward and Gowan, 1900).

In their cross sectional diameter and the thickness of their secondary walls the narrow tracheids in the spring wood resemble the summer wood tracheids. But, unlike the latter, the narrow tracheids generally have pits only on those areas of their walls that are in contact with the cells of xylem rays. A rough analogy with the fibers in the angiosperm woods would not be out of place; however, these tracheids have bordered pits on their walls, they also do not show any special intrusive apical elongation during their differentiation. As mentioned earlier, the narrow and the wide tracheids within a tier may show some apical elongation during

their differentiation, but, on the whole, their length corresponds to the length of the fusiform initial of the tier and there does not seem to be any correlation between the degree of apical elongation and the nature of the tracheid. It has been indicated by Bailey (1920b) that fluctuations in the length of tracheids in a tier may occur within a growth increment and from one growth increment to another. These fluctuations may be related to varying degrees of apical elongation of individual tracheids during their differentiation.

The indefinite arrangement of tracheids in radial files and occasional presence of groups of small tracheids interspersed among larger tracheids (FIG. 21) seem to be features typical of *Ginkgo* wood. The study of tiers reveals that these features have their basis in a combination of several factors — the presence of narrow tracheids interspersed among wide tracheids in the same tier, occasional radial divisions in the xylary initials and the differentiation of derivatives as narrow tracheids, presence of narrow tracheids in tangentially adjacent tiers, differential intrusive growth of the tips of the derivatives in a tier, and differential expansion of the wide tracheids during their maturation.

It has been shown in the present study that the axial parenchyma in the xylem of *Ginkgo* is formed with the decline of fusiform initials. The radial files of parenchyma cells are only the declining tiers in xylem and their appearance as radial plates of cells depends on the duration of time through which a fusiform initial declines and divides periclinally toward xylem. The declining tiers have no particular spatial relationship with the rays, as Tupper (1911) thought; parts of these tiers may be in contact with existing rays, other parts may not be so connected. Tupper's (1911) observation that the crystal-containing cells are modified parenchyma cells is acceptable, if one bears in mind that the differentiation of these cells is completed very close to the cambium. The lateral expansion of the crystal-containing parenchyma cells would be possible only in the plastic zone of differentiating tracheids, not in the mature wood.

A detailed study of the bark, including the cytology of sieve elements and albuminous cells, changes in the old phloem, seasonal changes, and the structure of the periderm was beyond the scope of the present work. Emphasis was placed upon the origin and the interrelationships of the phloem elements as they are derived from the cambial initials. These have been described in detail elsewhere in this paper. In the following paragraphs, therefore, only a few points concerning the declining tiers and the rays in the phloem of *Ginkgo* and Pinaceae are mentioned briefly.

Although the decline of fusiform initials and their conversion to ray initials is often well represented in the phloem of *Ginkgo*, it does not seem to be as extended as in the phloem of Pinaceae. As a result, the "radial plates of cells," described in the literature and later interpreted as the declining tiers in phloem (see Srivastava, 1962), are usually not as clearly marked in the phloem of *Ginkgo* as they are in the phloem of Pinaceae. However, such radial plates do occur and their derivatives, as in Pinaceae, include starch-containing and albuminous cells (FIG. 13).

It was shown in the Pinaceae (Srivastava, 1962) that the differentiation of albuminous and starch-containing cells is rather irregular among the early derivatives of new ray initials; but as the ray initials become well established, the derivatives of marginal initials differentiate preferentially as albuminous cells, while those of submarginal initials differentiate as starch-containing cells. With addition of new initials at the margins of existing rays, the derivatives of initials that now become submarginal start to differentiate as starch-containing cells. In *Ginkgo* the derivatives of ray initials as a rule do not include albuminous cells. The derivatives of marginal and submarginal initials differentiate as starch-containing cells only. It appears that in *Ginkgo*, in comparison to Pinaceae, not only is the decline of fusiform initials and their conversion to ray initials more abrupt, but the change from a production of albuminous cells to starch-containing cells is rather abrupt also.

A discussion of the inappropriate term *albuminous cell* has already been given and is not repeated (see Srivastava, 1962).

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EXPLANATION OF PLATES

The following symbols have been used consistently in all the plates: a, albuminous cell; c, cambial zone; cc, crystal cell; dt, declining tier; f, phloem fiber; nt, narrow tracheid; r, ray; s, sieve element; sc, starch-containing cell; sw, summer wood; wt, wide tracheid.

PLATE I

FIGS. 16–19. Transverse and tangential views of xylem, cambium and phloem. 16, Transverse section of old stem (Boston, 1961), × 70. 17, Transverse section of xylem of old stem (Boston, 1961) stained with phloroglucin–HCl and mounted in glycerine. Pith toward the bottom of the plate, × 115. 18, Tangential section of xylem of a young long shoot (Boston, 1961) showing transverse wall in a summer wood tracheid, × 390. 19, Radial section of xylem of old stem (A [wood coll.] 11353), × 190.

PLATE II

FIGS. 20–23. Xylem of old and young stems. 20, A radial file of tracheids isolated during maceration from an old stem (Boston, 1961). A variable number of narrow tracheids alternate with a varying number of wide tracheids, × 115. 21, Transverse section of xylem of old stem (A [wood coll.] 10138) showing a declining tier and narrow tracheids interspersed among wide tracheids; pith toward the bottom of the plate, × 80. 22, Transverse section of xylem of a young long shoot (A [wood coll.] 12048); pith toward the bottom of the plate, × 80. 23, Transverse section of a young long shoot (Boston, 1961), × 115.
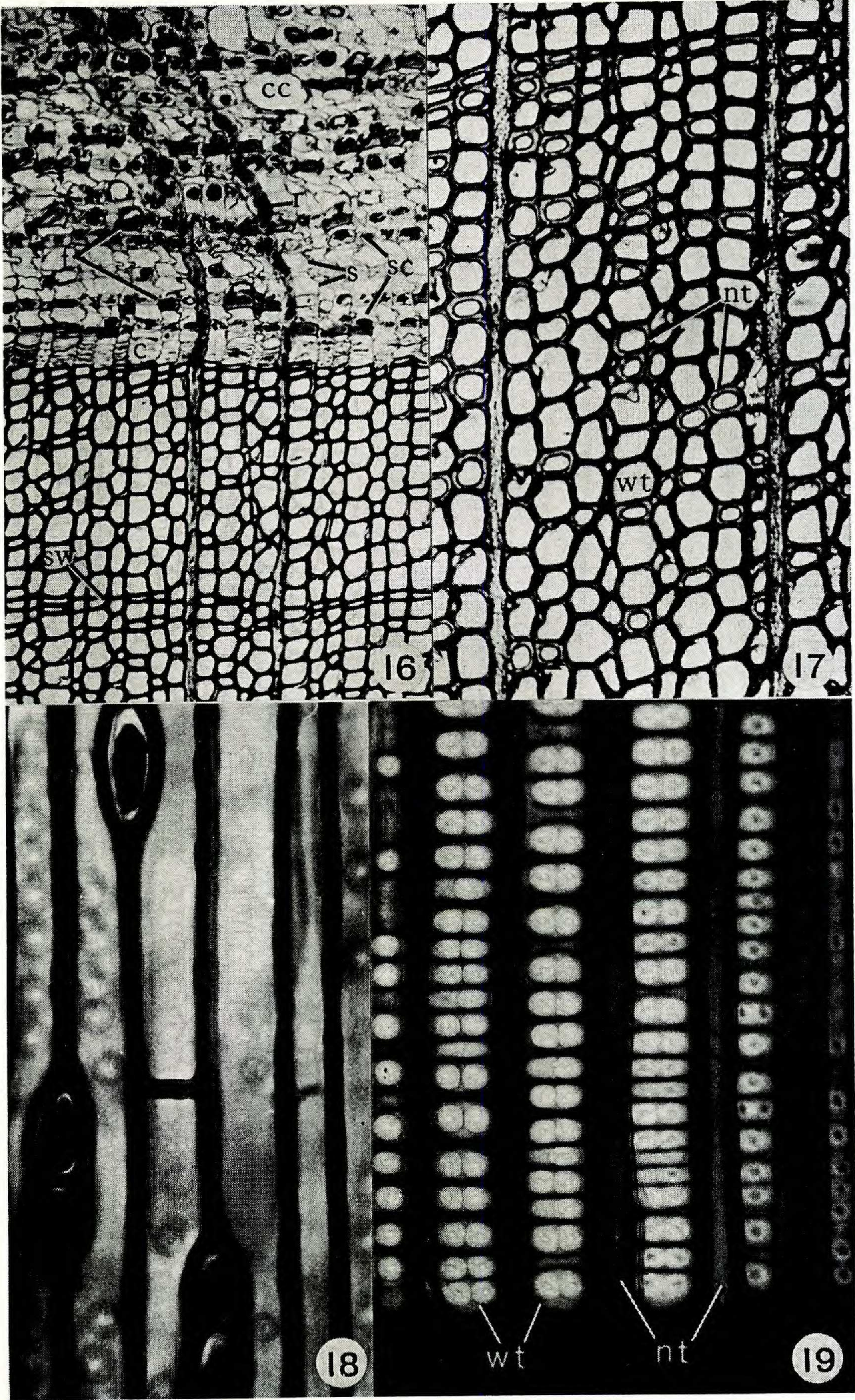
PLATE III

FIGS. 24–27. Transverse, tangential, and radial sections of xylem and phloem. 24, Transverse section of a short shoot (Boston, 1961), × 115. 25, Radial
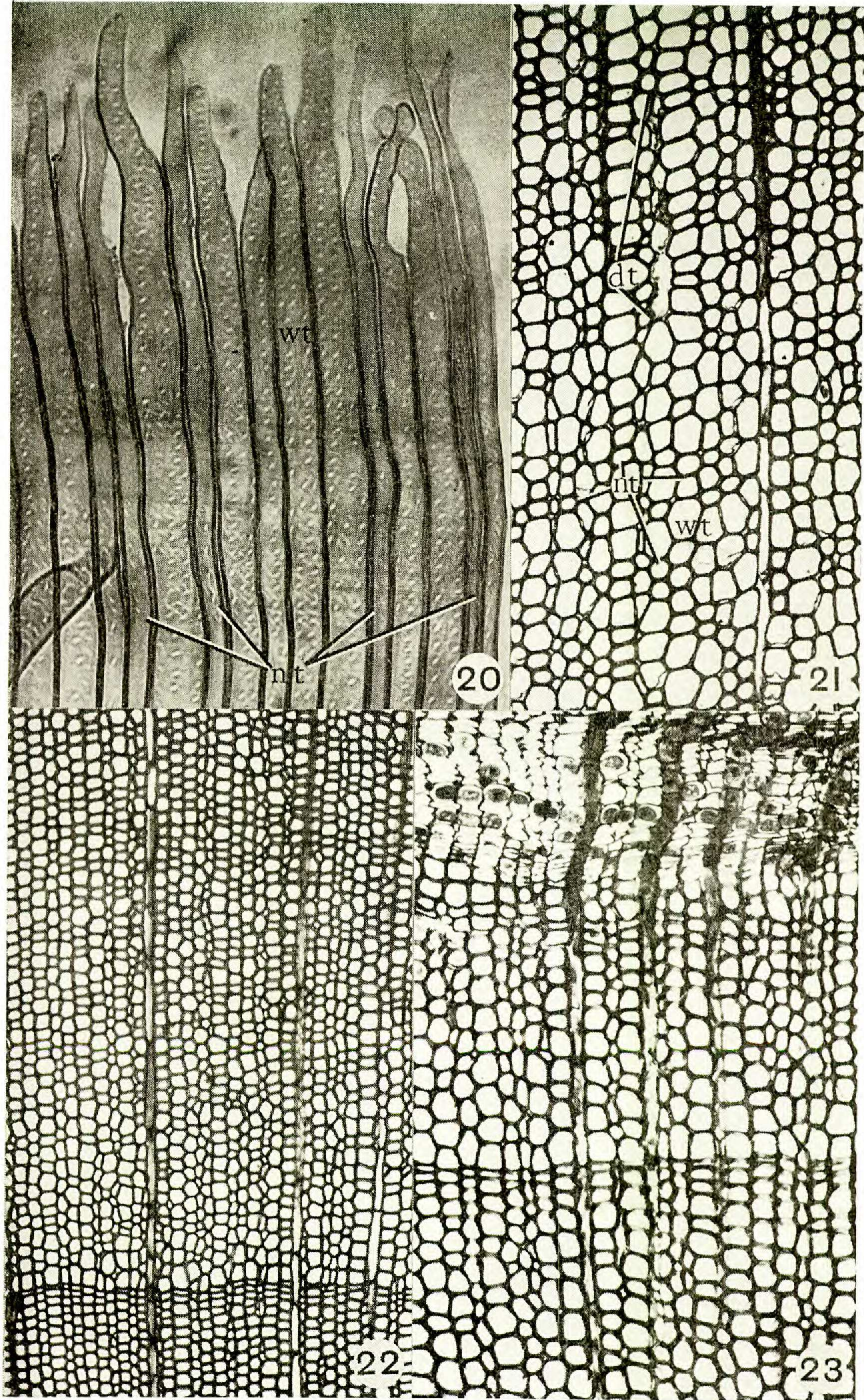
section of xylem of an old stem (Boston, 1961, Regaud's fixative) stained with IKI and mounted in glycerine. The section shows axial xylem parenchyma with crystal and starch-containing cells, × 85. 26, Tangential section of xylem of an old stem (Boston, 1961, Regaud's fixative) stained with Regaud's hematoxylin and showing axial parenchyma with crystal and starch-containing cells, × 70. 27, Radial section of latest xylem, cambium and phloem of an old stem (Boston, 1961, Regaud's fixative) stained with IKI and mounted in glycerine. Axial file of xylem-parenchyma cells containing druses of calcium oxalate and starch are seen next to the cambium. In the phloem, sieve elements and parenchyma strands with starch-containing cells and albuminous cells are seen, × 190.
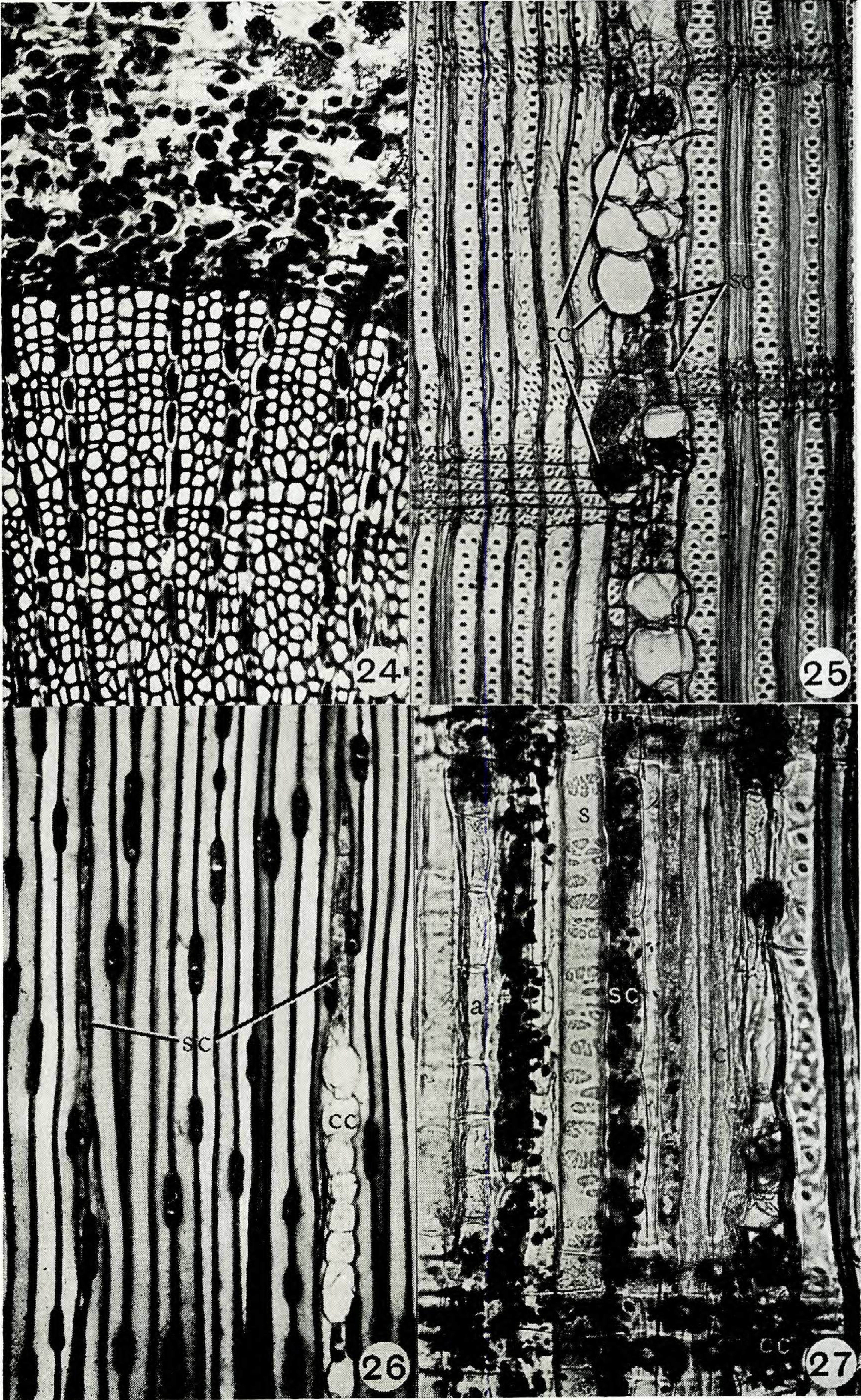
PLATE IV

Figs. 28–31. Radial and tangential sections of phloem of old stem. 28, Radial section (Boston, 1961, Regaud's fixative) stained with Hotchkiss method (see Glick, 1949, p. 44) showing sieve areas, × 780. 29, Tangential section of phloem close to the cambium (Boston, 1961, Regaud's fixative) stained with aniline blue and mounted in glycerine. The section shows albuminous cells and starch-containing cells in parenchyma strands, × 190. 30, Tangential section of old phloem (Boston, 1961, Regaud's fixative) stained with IKI and mounted in glycerine. Albuminous cells appear empty and some are collapsed; the starch-containing cells remain alive, × 190. 31, Tangential section of old phloem (Boston, 1961) showing phloem fibers and parenchyma strands, some cells of which contain druses of calcium oxalate, × 70.

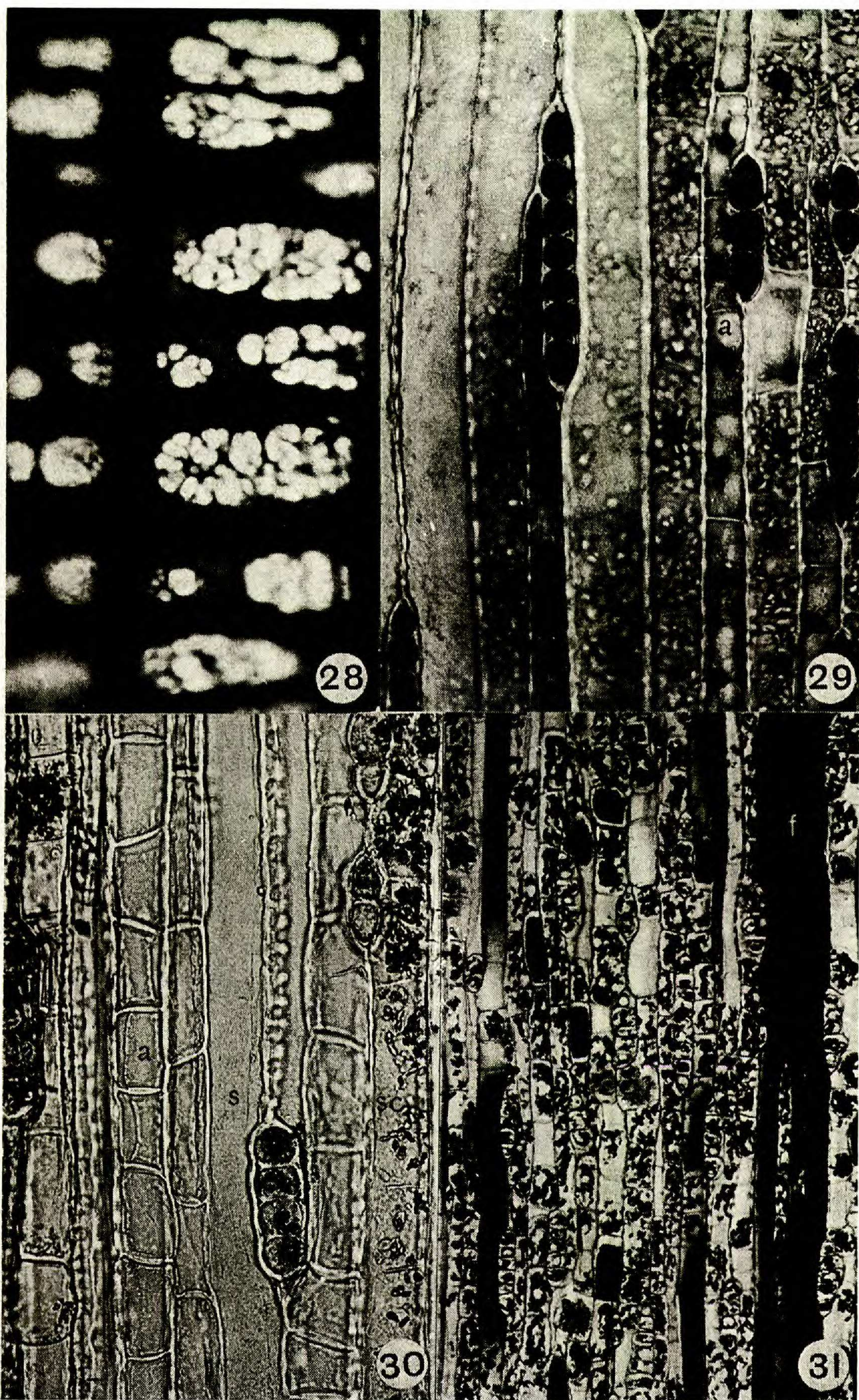SRIVASTAVA, GINKGO BILOBA

SRIVASTAVA, GINKGO BILOBA

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